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Facteurs influençant la régénération de deux espèces de *Physalis* à partir de fragment racinaires

A.E. Abdullahi et P.B. Cavers

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Résumé de l'article

Le coqueret glabre (*Physalis virginiana* var. *subglabrata*) et le coqueret hétérophylle (*P. heterophylla*) sont des mauvaises herbes indigènes, devenant plus répandues dans le sud de l'Ontario. Leur succès est dû en grande partie à la multiplication végétative, surtout lors de la dispersion des fragments racinaires pendant le travail du sol. Des fragments racinaires de longueurs différentes, échantillonnés à différents stades du cycle vital et provenant de parties différentes du système racinaire, furent plantés à différentes profondeurs et orientés en différentes positions, afin de déterminer le pourcentage de régénération sous des conditions naturelles et en serre. Aucun des fragments laissés à la surface du sol ne s'est régénéré. La régénération la plus rapide s'est produite à de faibles profondeurs (5 cm). La longueur minimum à laquelle la régénération fut observée était 2,5 cm. Le pourcentage maximum de régénération fut obtenu chez les fragments d'une longueur de 10 cm. Pour les deux espèces, l'orientation des fragments n'avait aucune influence sur la capacité de régéréation, ni le temps requis pour se régénérer. Pour les deux espèces, les fragments échantillonnés lors de la dispersion des fruits ont montré une régénération réduite (durant la même saison) comparativement à ceux échantillonnés tôt pendant le stade végétatif. Les fragments racinaires prélevés près du collet ont démontré le pourcentage de régénération le plus faible. Les fragments présentant des bourgeons lors de la plantation se sont régénérés plus rapidement que ceux dépourvus de bourgeons. En serre et sous conditions naturelles, les plantules de coqueret glabre ont émergé avant celles du coqueret hétérophylle. Ces résultats suggèrent que la réduction des infestations de coqueret serait possible en rapportant les fragments en surface lors du travail du sol.

Factors affecting regeneration from root fragments in two *Physalis* species

Adan E. Abdullahi and Paul B. Cavers[1]

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Smooth ground-cherry (*Physalis virginiana* var. *subglabrata*) and clammy ground-cherry (*P. heterophylla*) are native weeds that are becoming more common in arable land in southern Ontario. Much of their success stems from vegetative propagation, especially after dispersal of root fragments during cultivation. Root fragments of different lengths, collected at different life cycle stages, from different parts of the root system and replanted at different depths and orientations in the soil, were tested for regeneration in the field and the greenhouse. No fragments left on the soil surface regenerated. Shallow (5 cm) burial led to the fastest regeneration. Fragments as short as 2.5 cm regenerated but the highest percentage regeneration was from fragments 10-cm long. Orientation had no effect on the capacity of root fragments to regenerate nor on the time taken to regenerate in either species. In both species, fewer root fragments sampled from plants at the fruit dispersal stage regenerated in the same season than fragments obtained at the early vegetative stage. Root fragments obtained from parts of the root system closest to the crown had the least regeneration. Root fragments with preformed visible buds at planting time regenerated faster than those with no preformed buds. In both the greenhouse and the field, smooth ground-cherry shoots emerged faster than those of clammy ground-cherry. These results suggest that reduction in ground-cherry infestations could be achieved by cultivating and dragging fragments to the surface.

[Facteurs influençant la régénération de deux espèces de *Physalis* à partir de fragments racinaires]

Le coqueret glabre (*Physalis virginiana* var. *subglabrata*) et le coqueret hétérophylle (*P. heterophylla*) sont des mauvaises herbes indigènes, devenant plus répandues dans le sud de l'Ontario. Leur succès est dû en grande partie à la multiplication végétative, surtout lors de la dispersion des fragments racinaires pendant le travail du sol. Des fragments racinaires de longueurs différentes, échantillonnés à différents stades du cycle vital et provenant de parties différentes du système racinaire, furent plantés à différentes profondeurs et orientés en différentes positions, afin de déterminer le pourcentage de régénération sous des conditions naturelles et en serre. Aucun des fragments laissés à la surface du sol ne s'est régénéré. La régénération la plus rapide s'est produite à de faibles profondeurs (5 cm). La longueur minimum à laquelle la régéné-

1. Department of Plant Sciences, University of Western Ontario, London, Ontario, Canada N6A 5B7

ration fut observée était 2,5 cm. Le pourcentage maximum de régénération fut obtenu chez les fragments d'une longueur de 10 cm. Pour les deux espèces, l'orientation des fragments n'avait aucune influence sur la capacité de régénération, ni le temps requis pour se régénérer. Pour les deux espèces, les fragments échantillonnés lors de la dispersion des fruits ont montré une régénération réduite (durant la même saison) comparativement à ceux échantillonnés tôt pendant le stade végétatif. Les fragments racinaires prélevés près du collet ont démontré le pourcentage de régénération le plus faible. Les fragments présentant des bourgeons lors de la plantation se sont régénérés plus rapidement que ceux dépourvus de bourgeons. En serre et sous conditions naturelles, les plantules de coqueret glabre ont émergé avant celles du coqueret hétérophylle. Ces résultats suggèrent que la réduction des infestations de coqueret serait possible en rapportant les fragments en surface lors du travail du sol.

INTRODUCTION

Smooth ground-cherry [*Physalis virginiana* Mill. var. *subglabrata* (Mackenz. & Bush) U.T. Waterfall], and clammy ground-cherry (*P. heterophylla* Nees) are perennial herbs native to Canada and the United States (Gleason 1963). Smooth ground-cherry grows in corn (*Zea mays* L.), soybean [*Glycine max* (L.) Merr.] and tomato (*Lycopersicon esculentum* Mill.) fields, and in pastures. In Ontario, clammy ground-cherry grows in open woods, old fields, cultivated fields, roadsides, and railway embankments (Abdullahi *et al.* 1991). Both species are capable of regenerating from the root system, as well as reproducing through seeds (Abdullahi *et al.* 1991). Weed control specialists across southern Ontario have told us that both species pose increasing problems in cultivated land.

The resistance of the two species to control can be partially attributed to their deep and extensive root systems and to their ability to regenerate from buds produced adventitiously on their roots (Abdullahi 1993). Root buds on the intact plants are rather inactive. However, the growth of buds is stimulated when the plants are clipped or when the root system is fragmented through cultivation (Abdullahi 1993).

Although seeds can produce new infestations of clammy and smooth ground-cherry, the seeds are apparently less important in spreading the species than the roots (Abdullahi 1993). In intact plants, most shoots develop from underground stems or from the thick horizontal roots in the upper 20 cm of the soil. However, vertical and deep penetrating roots will also develop shoots after mechanical disturbance, *e.g.*, cultivation, if conditions are favourable (Abdullahi 1993).

Fragmentation releases the root buds from the influence of parts that have been removed (McIntyre 1972). Cutting the roots of leafy spurge (*Euphorbia esula* L.) stimulated the growth of buds in the region 2.5-5 cm below the cut (Coupland *et al.* 1955).

The capacity of root fragments to develop new shoots can be influenced by many factors. Differences in the regenerative capacity of root fragments, depending on their original position in the root system, have been reported in *Cirsium arvense* (L.) Scop. (Hamdoun 1972), *Chondrilla juncea* L. (Cuthbertson 1972), *E. esula* (Raju *et al.* 1964), and *Taraxacum officinale* Weber (Mann and Cavers 1979). Root fragments in a number of species exhibited different regeneration capacities at different times of the year and, therefore, during different growth stages, *e.g., Rubus idaeus* L. (Hudson 1953), *C. juncea* (Rosenthal *et al.* 1968), *Armoracia rusticana* Gaertn. (Dore 1953), *E. esula* (Raju *et al.* 1964), *T. officinale* (Mann and Cavers 1979). Leakey (1981) reviewed the factors that influence regeneration. In addition to position in the root system, growth stage and time of year, he mentioned resistance to rotting, size of fragment and frequency of parent plant defoliation prior to fragmentation.

Investigations on regeneration from root fragments are limited, and in no previous research was there a comparison of regeneration from root fragments in two closely related native species living in cultivated cropland. Investigations were conducted in 1991 and 1992 to determine the effects of size of fragment, depth in soil after fragmentation, root fragment orientation, plant growth stage at fragmentation, and original position of fragment in the root system, on the subsequent capacity of root fragments to regenerate in *P. heterophylla* and *P. virginiana* var. *subglabrata*.

MATERIALS AND METHODS

Source of materials

Roots of smooth ground-cherry were obtained from the J. Shaw farm near Ridgetown, Ontario (lat. 42°26' N, long. 81°54' W) from an extensive population in an arable field that had been planted to corn in 1990 and 1991. The field, with a loam soil, had been subjected to annual herbicide applications with metolachlor [2-chloro-*N*-(2-ethyl-6-methylphenyl)-*N*-(2-methoxy-1-methylethyl) acetamide] and atrazine [6-chloro-*N*-ethyl-*N'*-(1-methylethyl)-1,3,5-triazine-2,4-diamine] in 1990 and 1991 to control broad-leaved weeds.

Roots of clammy ground-cherry were collected from a large population in a sandy loam soil in a soybean field near Iona Station, Ontario (lat. 42°44' N, long. 81°27' W). The herbicide treatment applied in 1991 was imazethapyr [2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl]-5-ethyl-3-pyridinecarboxylic acid] and linuron [*N'*-(3,4-dichlorophenyl)-*N*-methoxy-*N*-methylurea] at recommended rates.

For the 1991 experiments (depth of burial, fragment size) roots were excavated directly from the above-mentioned field sites. For all other experiments, done in 1992, roots were collected from the two source populations in 1991 and established from 10-cm-long root fragments in field plots in a silt loam soil at the Environmental Sciences Western (E.S.W.) Field Station (lat. 43°4' N, long. 81°19' W) of the University of Western Ontario for smooth ground-cherry, and at the Ridgetown College of Agricultural Technology for clammy ground-cherry. At Ridgetown, a sandy loam site was used since clammy ground-cherry prefers sandy soils. For each collection date (natural and planted populations), roots were excavated from at least 10 randomly chosen points within the population.

General protocol

Root systems were excavated with the aid of a garden fork, placed in large plastic bags for transport to E.S.W., and prepared immediately for experiments. If necessary, the root systems were maintained in moist soil overnight, but in every experiment, fragments were replanted within 24 h of excavation.

In the greenhouse experiments, fragments were planted horizontally 5 cm below the soil surface in 20 cm diam plastic pots filled to 16 cm deep with potting soil (black muck:coarse sand:peat moss, 1:1:3 vol.). The pots were watered twice daily and given a fertilizer solution (N-P-K, 20-20-20) twice weekly. This solution also delivered chelated trace elements : iron, 0.1%; manganese, 0.05%; zinc, 0.05%; boron, 0.05%; and copper, 0.02%.

In the field plots at E.S.W., fragments were planted horizontally 7 cm deep (unless otherwise noted) in silt loam soil in rows 50 cm apart with 50 cm between fragments within rows. The plots were not irrigated but were handweeded frequently. Data on rainfall and minimum and maximum daily temperatures were recorded at E.S.W. for 1991 and 1992.

Unless otherwise noted, root fragments were taken from the uppermost 40 cm of the vertical roots (Abdullahi 1993) and underground stem tissues were excluded. Root fragment lengths were standardized at 10 cm, unless otherwise noted, with thicknesses ranging between 3 and 8 mm. In all experiments a completely randomized design was used.

Effects of depth of fragment burial and fragment length

Roots were collected on 10 July 1991 and taken to E.S.W. for fragmentation. Both experiments were run in field plots. For the depth experiment, fragments were left on the soil surface and buried 5, 10 and 15 cm deep with 20 fragments of each species at each depth. In the experiment with fragments of different lengths, the fragments were 2.5, 5.0, 7.5 and 10.0 cm long, with 20 fragments of each length. The number of fragments that had regenerated was recorded 17, 27 and 45 d after planting. At harvest (24 August 1991) plant height was measured from soil level to the growing point of the tallest shoot. Then, shoots were separated from roots at soil level and dried in an oven to constant weight, which was recorded.

Fragment orientation

This experiment was run in the field and repeated in the greenhouse. Root systems were collected on 15 July 1992. Five orientations were tested : a) horizontal; b) vertical, with the proximal end (proximal to the shoot) towards the soil surface; c) vertical, with the proximal end inverted; d) inclined at 45°, with the proximal end towards the soil surface; e) inclined at 45°, with the proximal end inverted.

Care was taken to ensure that at orientations other than horizontal, the uppermost tip of the fragment was buried to the proper depth (5 cm in the greenhouse and 7 cm in the field). Twenty fragments per treatment were used in both the greenhouse and the field experiments.

Percent regeneration and days to emergence were recorded. All visible preformed buds on each fragment were noted before replanting.

Growth stage at fragmentation

This experiment was run in the field and repeated in the greenhouse. Roots were excavated, fragmented and replanted at six different growth stages (20 fragments per stage in field, 20 in greenhouse) : a) early vegetative stage, plants had two or three leaves (10 May 1992); b) vegetative stage, plants had 8-12 leaves (10 June); c) flowering (30 June); d) fruit formation (24 July); e) fruit maturation (6 September); f) fruit dispersal (4 October). Percent regeneration, number of shoots emerged per fragment (greenhouse only) and days to emergence were recorded. Data were taken in the field throughout 1992. For later samples (stages d-f), regeneration was checked in the spring of 1993. Data for spring 1993 are not complete because of overwinter erosion and other disruptions to the plot area. In the greenhouse, observations were continued until 4 November 1992. Supplemental lighting from cool-white fluorescent plus incandescent bulbs was supplied in the greenhouse after early October 1992.

Fragments from different parts of the root system

This experiment was run in the greenhouse only. Root systems were collected at the flowering stage (2 July 1992). At this stage the plants had well-developed root systems with many visible buds, although the buds were distributed irregularly. Twenty fragments from each of the following parts (Abdullahi 1993) were used : a) underground stem; b) thick horizontal root without visible buds (50 cm from main stem); c) thick horizontal root with visible buds (50 cm from main stem); d) thick horizontal root starting 0-10 cm from main stem, without visible buds; e) thick vertical root with visible buds from older plants (> 2 yr); f) thick vertical root from 50 cm directly below the main stem, with visible buds; g) thick vertical root from 50 cm directly below the main stem, with no visible buds; h) thin root (1.5 mm diam) with no visible buds, distant from main stem; i) thin root (1.5 mm diam) with visible buds, distant from main stem. Percent regeneration and days to emergence were recorded.

Data analysis

Data on percent regeneration were tested by chi-square analysis (Cox 1987). The chi-square analysis was conducted on the number of fragments regenerated and non-regenerated out of the total (20) planted for each treatment. The results are reported as percentages. Analyses of variance of data on time taken from emergence were done by means of the general linear models procedure (SAS Institute Inc. 1990).

RESULTS AND DISCUSSION

Depth of burial

No root fragment left on the soil surface regenerated in either species. All of these fragments shrivelled and rotted. Similar results were obtained with rhizome fragments of *Achillea millefolium* L. (Bourdôt

1984), *Cyperus rotundus* L. and *Sorghum halepense* L. (Horowitz 1972). Mann and Cavers (1979) failed to get any regeneration of 2-cm long fragments of *Taraxacum officinale* (dandelion) laid horizontally on the soil surface in London, Ontario (lat. 43°1' N, long. 81°19' W) in July and August 1974. However, they did obtain 77.5% regeneration in the wetter month of August 1975. In another experiment we left fragments of both *Physalis* species on the surface at other times of the year but none regenerated.

Fragments of both species buried 5 cm deep regenerated more quickly than those buried 15 cm deep (Table 1), but there were no significant differences between the depth treatments in percent regeneration at the end of the experiment 45 d after planting (Table 1). Slower regeneration from greater depths has been recorded for other perennial species (Hamdoun 1972; Swanton 1986). There were no significant differences between the 5, 10 and 15-cm burial treatments in height or shoot dry weight.

Fragment length

In both species, fragments as short as 2.5 cm regenerated. For clammy ground-cherry a significantly higher total percent regeneration was obtained from fragments 10 cm long than from shorter fragments (Table 2). For smooth ground-cherry, there were no significant differences in total percent regeneration at 45 d after planting among the different fragment lengths (Table 2). In other species such as *Saponaria officinalis* L. (Lubke and Cavers 1970), *T. officinale* (Mann and Cavers 1979) and *Cirsium vulgare* (Savi) Ten. (Hamdoun 1972), longer or thicker fragments were more likely to regenerate than shorter thinner ones. Regeneration has been obtained from even shorter fragments in other species. For example, Healy (1953) found that 1 cm long fragments from all parts of the root system of *T. officinale* were able to regenerate and Chancellor (1956) obtained regeneration from 1 cm long segments of *Rumex crispus* L. rootstocks taken at least 12 cm below ground.

In both species, the first shoots emerged from 10-cm root fragments. There were no significant differences among the fragments of different length in either dry weight or height of shoots after regeneration.

Fragment orientation

Orientation had no significant effect on the capacity of root fragments to regenerate in either species nor on the time taken to regenerate. Clammy ground-cherry root fragments took significantly longer to regenerate in the greenhouse than those of smooth ground-cherry regardless of planting orientation, but this difference was not seen in results from

Table 1. Cumulative emergence of clammy and smooth ground-cherry root fragments[1] planted at different depths in the field

Depth of planting (cm)	Cumulative emergence (%)		
	17 DAP[2]	27 DAP	45 DAP
Clammy ground-cherry			
0	0 b[3]	0 b	0 b
5	55 a	60 a	60 a
10	15 b	40 a	60 a
15	5 b	5 b	45 a
Smooth ground-cherry			
0	0 b	0 b	0 b
5	30 a	75 a	75 a
10	15 ab	40 a	70 a
15	5 b	15 b	65 a

[1] n = 20 fragments per treatment.

[2] DAP : days after planting.

[3] Numbers within the same column for each species followed by the same letter are not significantly different at the 5% level of probability according to chi-square analysis.

Table 2. Cumulative regeneration of clammy and smooth ground-cherry from root fragments[1] planted at different depths in the field

Fragment length (cm)	Cumulative regeneration (%)		
	17 DAP[2]	27 DAP	45 DAP
Clammy ground-cherry			
2.5	10 b[3]	25 b	25 b
5.0	5 b	30 b	30 b
7.5	25 b	30 b	40 b
10.0	65 a	95 a	100 a
Smooth ground-cherry			
2.5	25 ab	50 a	50 a
5.0	35 ab	50 a	70 a
7.5	15 b	70 a	70 a
10.0	40 a	65 a	65 a

[1] n = 20 fragments per treatment.
[2] DAP : days after planting.
[3] Numbers within the same column for each species followed by the same letter are not significantly different at the 5% level of probability according to chi-square analysis.

the field. Root fragments with preformed visible buds at planting time regenerated faster than those with no preformed buds.

Examination of the root fragments 4-5 wk after planting indicated that the site of shoot emergence from a fragment generally depended on the location of visible buds prior to planting. However, in root fragments with no preformed visible buds more shoots developed from the proximal end (closer to the crown) and more roots from the distal end.

These results suggest that both species will be capable of regenerating from root fragments after tillage operations, regardless of how the fragments are repositioned in the soil, provided they are covered. In contrast, Mann and Cavers (1979) observed reduced regenerative capacity in root fragments of *T. officinale* that were planted in orientations other than the normal vertical direction. However, *T. officinale* lacks the horizontally spreading thick roots characteristic of ground-cherry species and many other perennial herbs.

In several cases, shoots developing from preformed visible buds took longer to emerge from the soil if those buds were located on a root section oriented upside down. These results agree with those of Richardson (1975) working on *Rubus procerus* P.J. Muell. Richardson also reported that shoots could arise at any position along the root segments, but a greater number emerged from the proximal end (nearest the stem). Raju *et al.* (1964) obtained a similar result with *Euphorbia esula* where the first shoot usually arose from the proximal end of the fragment. Both species of ground-cherry had shoot patterns similar to those of *R. procerus* and *E. esula*.

Growth stage at fragmentation

In both species, significantly fewer root fragments from plants at the fruit dispersal stage regenerated in the same season in the greenhouse, compared to those from plants at the early vegetative stage (Table 3). In the field, no fragment from plants dispersing fruit (in October) regenerated in the same year. From the sampling at fruit maturation, fewer fragments of clammy ground-cherry regenerated in the field than for smooth ground-cherry. Percent regeneration of fragments of smooth ground-cherry taken at the early vegetative stage was lower than that recorded for fragments taken during fruiting.

The results from the greenhouse (Table 3) demonstrate that fragments of both species, sampled in any month of the growing season, can regenerate under favourable conditions. In the field, however, fragments taken at the end of the season could not regenerate in the same season (Table 3). Some of these frag-

Table 3. Percent regeneration of root fragments[1] of clammy and smooth ground-cherry sampled at different growth stages, in greenhouse and field plots

		Regeneration (%)			
	Date of sampling in	Greenhouse		Field	
Growth stage	1992	CGC[2]	SGC	CGC	SGC
Early vegetative	10 May	100 a[3]	100 a	70 a	55 b
Vegetative	10 June	100 a	85 ab	85 a	65 ab
Flowering	30 June	85 ab	95 a	75 a	75 ab
Fruiting	24 July	70 b	90 ab	90 a	90 a
Fruit maturation	6 September	90 a	85 ab	30 b[4]	70 ab
Fruit dispersal	4 October	60 b	65 b	0 c[4]	0 c[4]

[1] n = 20 fragments per treatment.
[2] CGC = clammy ground-cherry; SGC = smooth ground-cherry.
[3] Numbers within the same column followed by the same letter are not significantly different at the 5% level of probability according to chi-square analysis.
[4] Some of these fragments regenerated the following year.

ments regenerated in the following spring but soil erosion that uncovered some fragments, moved others and buried some deeper, obviously altered our results. The low regenerative capacity recorded in the field for fragments of clammy ground-cherry taken at the fruit maturation stage matched the observed performance of above-ground shoots of this species. In southwestern Ontario, most shoots of clammy ground-cherry die before those of smooth ground-cherry, which often remain alive until late November. On the other hand, percent regeneration of fragments of clammy ground-cherry remained high during dry weather early in the season, whereas percent regeneration of smooth ground-cherry was slightly but significantly lower at the early vegetative stage than later in the season. Clammy ground-cherry is more common on well drained to droughty soils than smooth ground-cherry (Abdullahi *et al.* 1991).

Researchers working with other species (Cuthbertson 1972; Dore 1953; Mann and Cavers 1979; Raju *et al.* 1964) observed decreased shoot emergence from root fragments taken at the flowering stage. This can lead to reduced percent regeneration of fragments, especially if they are small or short (Mann and Cavers 1979) but Monson and Davis (1964), working with longer root fragments (about 12 cm long) of *Euphorbia* spp. reported a high incidence of emergence from fragments taken at all sampling dates throughout the growing season. Raju et al. (1964) recorded a significant drop at the flowering stage in mean number of shoots per fragment of *E. esula* but still obtained 1.6 shoots per 5-cm long fragment, enough to allow regeneration of most fragments. We did not record the number of shoots per fragment in this experiment but most of our 10-cm fragments produced two or more shoots.

In both greenhouse and field plots, smooth ground-cherry shoots emerged faster than those of clammy ground-cherry (Table 4). Significant differences in time from planting to shoot emergence were observed among the fragments from different growth stages. In the greenhouse, roots sampled at the early vegetative stage (when the plants had two to three leaves) regenerated in about 1 wk, whereas roots sampled at the beginning of fruit formation and thereafter took about twice as long to regenerate. For smooth ground-cherry, the pattern observed in time taken for fragments to regenerate in the field was the reverse of that in the greenhouse. This probably resulted from the rather dry weather early in the season and the greater rainfall in the later summer months recorded at

Table 4. Effect of growth stage at root fragmentation[1] on average time for shoot emergence of clammy and smooth ground-cherry

	Average time for shoot emergence (d ± SE)[2]					
	Clammy		Smooth		Both species combined	
Growth stage	Greenhouse	Field	Greenhouse	Field	Greenhouse	Field
Early vegetative	8.10±0.64	21.21±1.07	6.30±0.64	22.18±1.21	7.20±0.45	21.70±0.81
Vegetative	9.20±0.64	18.70±0.97	9.18±0.69	21.29±1.07	9.18±0.47	20.00±0.72
Flowering	9.47±0.70	21.20±1.03	7.90±0.66	18.27±1.03	8.71±0.48	19.73±0.73
Fruiting	14.64±0.77	19.83±0.04	10.44±0.68	13.11±0.94	12.54±0.51	16.47±0.67
Fruit maturation	14.17±0.68	18.00±1.63	12.41±0.70	15.43±1.07	13.29±0.48	16.71±0.98
Fruit dispersal	15.36±0.86	- -[3]	12.69±0.80	- -	14.03±0.59	- -
All stages combined	11.82±0.29	19.79±0.52	9.82±0.28	18.05±0.48		

[1] n = 20 fragments per treatment.
[2] (d + SE) = average ± standard error.
[3] - - : no shoot emergence from this treatment in 1992.

E.S.W. in 1992. In the field, clammy ground-cherry roots regenerated most quickly when sampled from plants at the fruit maturation stage, and smooth ground-cherry roots regenerated most quickly when sampled at the fruit formation stage. In the greenhouse, both species regenerated most rapidly from fragments sampled at the 2-3-leaf stage. Shoots emerging from root fragments sampled at the fruiting, the fruit maturation and fruit dispersal stages grew more slowly than those from fragments taken at preceding stages (data not shown).

Fragment origin within the root system

Fragments from all parts of the root system were able to regenerate (Table 5). Respectively, 91 and 96% of root fragments with visible buds regenerated in samples from clammy and smooth ground-cherry, whereas only about 48% of those without visible buds did so in either species. Root fragments as thin as 1.5 mm diam regenerated almost completely if they had preformed visible buds at planting and about 40% regenerated if they had no preformed buds at planting. Root fragments from 2-yr-old root systems also had strong regenerative capacity. Hamdoun (1972) obtained similar results with *Cirsium arvense* for fragments with and without visible buds. In both *Physalis* species, root fragments obtained from 50 cm deep on vertical roots had fewer preformed buds than those originating closer to the soil surface. Raju *et al.* (1964) noted a similar trend for *Euphorbia esula, i.e.*, more preformed buds and shoots on fragments taken from nearer the surface. However, root fragments of *E. esula* taken from all depths had strong regenerative capacity regardless of the presence of preformed buds.

Several authors have noted a reduced regenerative capacity from younger or thinner roots (Hamdoun 1972; Mann and Cavers 1979; Pegtel 1976). Pegtel (1976) suggested that root volume, and thus stored carbohydrate reserves, is the most important factor controlling shoot regeneration in *Sonchus arvensis* L. In *Physalis* species, this factor is obviously important for fragments without preformed visible buds.

The low regenerative capacity of fragments from horizontal roots close to the main stem in both *Physalis* species may reflect an adaptation that has value in an undisturbed root system. In both species, new daughter shoots do not emerge until the parent shoot has passed the stage of flower bud formation, and then at a spacing of about 30 cm or more from that parent shoot (Abdullahi 1993). This pattern of shoot emergence prevents competition with the original shoot for resources such as light, water and mineral nutrients.

Table 5. Effect of origin of root fragments[1] on their subsequent capacity to regenerate in smooth and clammy ground-cherry; regeneration in greenhouse

	Emergence (%)	
Origin of rootstock	CGC[2]	SGC
Underground stem	80 ab[3]	100 a
Thick horizontal root without buds (50 cm from main stem)	65 bcd	60 b
Thick horizontal root with buds (50 cm from main stem)	100 a	95 a
Thick horizontal root close to main stem without buds (0-10 cm from main stem)	35 d	35 b
Old thick vertical root fragment with buds	85 ac	90 a
Thick vertical root without buds (50 cm deep)	50 d	60 b
Thick vertical root with buds (50 cm deep)	100 a	100 a
Thin root with no buds (1.5 mm diam)	45 d	35 b
Thin root with buds (1.5 mm diam)	90 a	95 a

[1] n = 20 fragments per treatment.
[2] CGC = clammy ground-cherry; SGC = smooth ground-cherry.
[3] Numbers within the same column followed by the same letter are not significantly different at the 5% level of probability according to chi-square analysis.

In general, root fragments with visible buds produced shoots faster than those without visible buds (Table 6) but this did not apply to the thick horizontal roots. In the thick root category, fragments with no visible buds, taken 50 cm deep from the vertical taproot were the last to regenerate in both species (Table 6). Thin root fragments (1.5 mm diam) with no visible buds took about 20 d to produce shoots.

Morphological and physiological considerations

Hudson (1955) described seven types of regeneration from roots. Of these, Leakey (1981) found that three are relevant to weed species : a) suckers growing from uninjured roots at a distance from the parent plant; b) suckers developing on undisturbed roots after damage to or removal of shoots; and c) suckers growing from disturbed root fragments. Both smooth and clammy ground-cherry exhibit all three of these types of regeneration.

Both species of ground-cherry are similar to many other perennial weeds in that they produce preformed buds on the root system, comparatively few of which will develop into shoots on an intact plant. Leakey (1981) described the strong apical dominance found in intact root systems and postulated that it aids lateral spread by conserving assimilates for the growth of primary apices. The dormant preformed buds constitute a "bud bank" that can be of vital importance in regeneration of fragments after they have been severed from the larger system (Leakey 1981). Root fragments of ground-cherry are like those of leafy spurge (Raju *et al.* 1964) in that they can have several shoots develop but there is a tendency for buds at the end of the fragment nearest the main stem of the original plant to develop first and most vigorously. Fragments from ground-cherry also resemble those from leafy spurge (Raju *et al.* 1964) in that the capacity of a fragment to regenerate is not dependent on the presence of preformed shoot buds.

Leakey (1981) reported that the ability of a root fragment to resist decay varied greatly among different species. Fragments of both ground-cherry species remained alive in the soil for up to 8 mo before regenerating after a winter. We did not leave fragments for longer periods in the soil.

Table 6. Effect of origin of root fragments[1] on mean time to shoot emergence of clammy and smooth ground-cherry; regeneration in greenhouse

Origin of rootstock	Mean time to shoot emergence (d ± SE)[2] CGC[3]	SGC
Underground stem	9.56 ± 0.72	7.05 ± 0.64
Thick horizontal root without buds (50 cm from main stem)	6.38 ± 0.79	9.33 ± 0.74
Thick horizontal root with buds (50 cm from main stem)	7.45 ± 0.64	7.00 ± 0.66
Thick horizontal root close to main stem without buds (0-10 cm from main stem)	10.14 ± 1.08	7.29 ± 1.08
Old thick vertical root fragment with buds	8.82 ± 0.69	6.94 ± 0.68
Thick vertical root without buds (50 cm deep)	12.30 ± 0.91	9.50 ± 0.83
Thick vertical root with buds (50 cm deep)	7.45 ± 0.64	6.60 ± 0.64
Thin root with no buds (1.5-mm diam)	21.22 ± 0.95	20.14 ± 1.08
Thin root with buds (1.5-mm diam)	6.84 ± 0.66	7.47 ± 0.66

[1] n = 20 fragments per treatment.
[2] (d ± SE) = average ± standard error.
[3] CGC = clammy ground-cherry; SGC = smooth ground-cherry.

Implications for control in arable land

Our observations of fields in southern Ontario infested with clammy or smooth ground-cherry have revealed clear evidence of new infestations of both species arising from root fragments, often at a distance of several meters or more from an established clump. The ability to regrow at any time in the growing season, from any orientation within the soil, is important.

Destruction of root fragments could be achieved if they could be brought to the soil surface. Even if some fragments remain shallowly buried, this could be advantageous, since they would regenerate more quickly than more deeply buried ones. Quick regeneration could be followed by herbicide application, possibly before the crop is sown or before the crop plants are large enough to be damaged by inter-row passes by farm machinery.

Fragmentation of clammy ground-cherry clumps in the autumn may be more successful for control than it would be for smooth ground-cherry. Conversely, fragmentation of smooth ground-cherry clumps during dry periods could be more effective as a control than a similar measure against clammy ground-cherry.

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